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Modeling the animal in its world and the canonical problem for habitat selection

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Abstract Behavioral and evolutionary ecology made enormous progress in the last 50 years by using the assumption that the modeler/observer is external to the organism and its environment. This allows specifying details of the environment (e.g. predation risk or the probability of finding food) and then using a fitness optimization model to predict the behaviors that are the end point of natural selection. Doing so can be called the third-person perspective of the organism. More than 80 years ago, Jakob von Uexküll argued that a first-person perspective is possible if we replace the external observer's description of the environment by the organism's subjective characterization of itself and its surroundings based on its sensory data, and allow those sensory data to shape behavior. The first-person umwelt model becomes an evolutionary one when the genes determining the sensory responses evolve. I use a canonical problem of habitat selection (which will always be an important problem in biology and which was one of Leon Blaustein's favorite topics of research) to illustrate construction of first-person umwelt and third-person fitness optimization models. A canonical problem is the simplest but still interesting form of a collection of similar problems, with a focus on what is essential to the collection as a whole. In particular, a canonical problem does not model any particular situation, but has much in common with many situations. Here, the canonical problem focuses on an organism that needs to find a refuge from a harsh environmental season that begins at a fixed time when refuges vary in the level of protection from the harsh environment. Individuals who survive the harsh environmental season successfully reproduce. When searching for refuges, organisms experience predation risk so that the third-person fitness optimization model answers "when an organism encounters a habitat of a specific quality at a given time, is it predicted to settle or continue searching"? The first-person umwelt model is based on the assumptions that i) the organism has sensory inputs that provide information on quality of a habitat (settling is more likely in higher quality habitats) and the remaining time before the onset of the harsh environmental season (settling is more likely when less time remains), ii) the sensory information is combined to determine behavior, and iii) the genotypic architecture underlying the sensory functions evolves by natural selection. After developing predictions from the models by simulating populations following the rules developed from each, I use effect size measured by Cohen's *d* to explore how evolution of the genes of the response functions in the first-person umwelt model affects survival and convergence of the predictions of the first-person umwelt and third-person fitness optimization models.

Keywords behavior; habitat selection; fitness optimization; stochastic dynamic programming; umwelt; sensory inputs

To the memory of Leon Blaustein, a dear friend and wonderful colleague

Introduction

Habitat selection will always be an important problem in ecology and evolutionary biology (Morris, 2011; Northrup et al., 2022) and was one of Leon Blaustein's favorite topics. I had the great pleasure of discussing habitat selection with him for more than 30 years (Figure 1) leading to publications in behavioral, community, and population ecology (Blaustein et al., 2004; Eitam et al., 2002, 2003; Kiflawi et al., 2003a, 2003b, Sadeh et al., 2009; Segev et al., 2009, 2011). In this paper, I focus on the behavioral ecology of habitat selection because the population and community ecological effects of habitat selection must begin with the individual (Piper, 2011).

First-person and third-person models in behavioral and evolutionary ecology

One reason for the great advances in behavioral ecology in the last 50 years was and still is the focus on the third-person perspective when modeling behavior. In the third-person perspective, we specify an environment, typically describe an organism by "it" and ask the question "how do we predict its behavior" as shorthand for "how do we predict natural selection will act on the suite of available

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Figure 1. Left panel: Leon Blaustein and me in 1987, discussing whether re-flooding the Hula Valley would provide habitat for malarial carrying mosquitos and if yes, could they re-establish in Israel? Right panel: Together in 2000 preparing experimental habitats for the habitat selection work reported in Kiflawi et al. (2003a, 2003b).

behaviors?". We then use one of the modeling approaches for fitness maximization (e.g., the Euler-Lotka equation, rate-maximizing optimal foraging theory, age and/or state-dependent life history theory, frequency-dependent game theory, or sometimes individual-based models [see Giske et al., 2025 for more details]) to predict the behaviors that are the end points of natural selection. This is a very powerful paradigm for understanding observations and making testable predictions. In general, third-person perspectives focus on ultimate considerations and do not model proximate mechanisms, but there are exceptions (Mangel and Satterthwaite, 2008; McNamara and Houston, 2009).

An alternative is the first-person perspective (Roitberg, 1985; Ginsburg and Jablonka, 2019) in which the operative question is "What should I [the organism] do at this time, in this environment given my physiological state?". The philosopher Thomas Nagel discussed the perspective more than 50 years ago by asking "What is it like to be a bat?" (Nagel, 1974) and concluded that we could never know. Harari (2017, pg 362ff) agrees with that conclusion, but Dacey (2025) is not so sure.

Jakob von Uexküll (von Uexküll, 1934/2010) argued that a first-person perspective is possible if we replace the third-person observer's description of the environment by the organism's subjective model of itself and its surroundings, based on its sensory data. He called this approach "umwelt" from the German word meaning environment, with the understanding that we need to focus on how individuals of a particular species experience the world via their sensory systems. While the third-person perspective is general [e.g., the Marginal Value Theorem (Charnov, 1976; Mangel, 2006)], the first-person perspective is idiosyncratic, but that does not prohibit the construction of first-person models (Giske et al., 2013, 2014). General introductions to von Uexküll's ideas can be found in Kohl and Kohl (2000) and Yong (2023), and to first-person perspectives more technically in Budaev et al. (2019, 2024). The first-person model becomes an evolutionary one the genes determining the sensory responses evolve (Giske et al., 2013, 2014).

An example of the difference between the two perspectives is provided by the work of Schmidt and Smith (1987, and references there-in) on egg laying by the parasitoid wasp *Trichogramma minutum*. All else being equal, parasitic wasps lay more eggs in larger hosts. With the third-person perspective, specifying the environment means describing the distribution of the sizes of hosts, the number and size of offspring emerging from a host of a given size, and the rate of natural mortality. We can then develop models to predict the number of eggs laid in hosts of different sizes as a function of time in the reproductive season and the egg complement of the wasp. A simple metric of fitness (Charnov and Skinner, 1984, 1985) is the number of offspring emerging from a host of a particular volume as a function of the number of eggs laid in that host; a more complicated metric is the number of grand-offspring as a function of number of eggs laid (Clark and Mangel, 2000, Chapter 4). One can then use a third-person model, such as rate maximizing (Charnov and Skinner, 1984, 1985) or state dependent life history theory implemented by Stochastic Dynamic Programming (Mangel, 1987; Mangel and Clark, 1988) to predict the number of eggs laid in hosts of different volumes, and compare theory and empirical results (Mangel and Clark, 1988, Chapter 4; Clark and Mangel, 2000, Chapter 4).

In a first-person perspective, we ask how the wasp knows the size of a host and how many eggs it has. Schmidt and Smith (1987) showed that *Trichogramma* use relative curvature – determined as they walk along the host surface – to provide a measure of host volume. Schmidt and Smith (1987) furthermore provided a specific mechanism for the measurement of curvature: that the wasp determines curvature by detecting changes in the scapal-head angle of the antennae. Consistent with the idiosyncratic nature of the first-person model, they wrote: “It is particularly significant that this mechanism depends upon the size of the wasp and its appendages relative to the curvature of the host surface … it cannot provide information about the absolute curvature or diameter of a host” (Schmidt and Smith, 1987, pg 162–163). Similarly, stretch receptors in the abdomen of the wasp provide a sense of its egg complement. It also appears that these parasitoids recognize relatively short time intervals (Schmidt and Smith, 1987a), in that *Trichogramma* lay more eggs in a host egg when it takes more time to walk on it even if there is little or no change in curvature (Parent et al., 2016).

It is important to recognize from the outset that the difference between first and third-person models is not the difference between proximate explanation and ultimate explanation. Rather, it is a difference of how the observer/modeler is involved. In third-person models, the observer/modeler is external to the organism and its environment, which allows us to proceed with a model based on fitness maximization. In first-person models, the observer/modeler is internal to the organism, which receives signals from itself and the environment that guide its behavior. In this regard, the difference between first and third-person models echoes some of the issues in modern cosmology and the difference between the way that Newton (third-person) and Leibniz (first-person) viewed the world (Smolin (1997), pgs. 213–232, 260ff).

A canonical problem (Mangel, 2015) is the simplest but still interesting form of a collection of similar problems, with a focus on what is essential to the collection as a whole. Thus a canonical problem does not model any particular situation, but has much in common with many situations. Two other canonical problems in behavioral ecology – activity choice and resource allocation – are discussed in Mangel (2015).

Although he was not a modeler, Leon Blaustein deeply appreciated what models could do to support and enhance biological research. We also had many conversations about how to confront models and data. He really loved the notion of the Akaike Information Criterion (AIC); AIC-like ideas appear in Saward-Arav et al. (2016). There are no empirical data in this paper, but because of two modeling frameworks, we require a method for comparing predictions from the two models. As explained below, this will be done using effect size (Cohen’s *d*).

Overview of the paper

In the canonical problem in habitat selection, an individual must select a refuge allowing it to survive a harsh environmental season before reproduction. In particular, we will characterize survival while searching for a refuge prior to the onset of the harsh environment, the distribution of refuges of different quality, and survival during the harsh environmental season as a function of the quality of the refuge.

The third-person fitness optimization model is a straightforward application of Stochastic Dynamic Programming (SDP; Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000). The SDP model leads to a boundary in the plane determined by time and refuge quality (henceforth the time/quality plane) that separates regions in which the focal individual is predicted to settle from those in which it is predicted to continue searching. This boundary curve allows us to simulate by Monte Carlo methods the behaviors of a large number of individuals who randomly encounter habitats while experiencing mortality risk, and who settle in the encountered habitat or continue searching. We thereby obtain distributions of the times of death and settlement.

The first-person umwelt model begins with the assumption that the behavior of an individual is determined by the response to sensory signals from the environment and its physiology. For the canonical problem, we model a response to quality in which a stronger response means that the individual is more likely to settle and a response to time in which a stronger response means that the individual is more likely to continue searching. We assume that these are sigmoidal functions (Marreiros et al., 2008; Rasamoelina et al., 2020; Sharma et al., 2020) of the relevant variable (quality or time), in which evolved genes determine the strength of the response. By comparing the two responses, we predict whether the focal individual settles in the encountered habitat or continues to search. Forward simulation, also by Monte Carlo methods, allows us to obtain distributions of times of death and settlement, as in the third-person model.

The first-person umwelt model becomes an evolutionary model when natural selection acts on the genotypic architecture of the response functions. I use an extension of the equations of classical quantitative genetics, in which the values of offspring genes are the midpoint of the parental values modified by a Gaussian term (the classical equation) and then further modified by a uniformly distributed random variable as a proxy for a full genetic algorithm. For simplicity, I assume strong density dependence acting on the offspring of surviving individuals, so that population size is constant across generations.

For the first-person umwelt model itself, we can ask if evolution of the genes of the response functions increases survival. Each simulation of N individuals gives a single value of the number of individuals surviving to reproduce, and thus an estimate of the probability of survival to reproduction. We can then compare the fraction of individuals surviving in the initial generation, when the distribution of genotypes is random by assumption, and subsequent evolved generations. When survival in the evolved generations is greater than that in the initial generation, we conclude that evolution of the genes in the response function affects survival to reproduction.

Both the first-person umwelt and the third-person fitness optimization model produce (in every generation for the first-person umwelt model) distributions of the times of death and settlement. We can assess if the predictions of the first-person umwelt model are converging to the evolutionary endpoint predicted by the third-person fitness optimization model if the “distance” between the distributions for times of death and settlement are closer in evolved generations than in the initial generation. To do so, we use the measure of effect size Cohen's *d* (Cohen, 1988, 1994; Nakagaw and Cuthill, 2007; Nakagawa et al., 2017; Methratta, 2025).

I show that evolution of the genotypic architecture of the response functions leads to increased survival. Evolution is rapid with gene distributions stabilizing in 20–25 generations or less. Genetic variation is maintained or lost according to parameters characterizing inheritance. I then use Cohen's *d* to show that, as a result of the evolution of genes in the response functions, the first-person umwelt model makes predictions concerning times of death and settlement converging to those of the third-person fitness optimization model.

I begin the **Discussion** by noting that the first-person umwelt model does not require assuming that the organism knows the rate of mortality (as a third-person fitness optimization model does), with implications for a changing environment. I then discuss possible extensions of the models such as including state variables, using offspring production rather than parental survival as the metric of Darwinian fitness, including additional mortality by a secondary predator that is not present all of the time but only sporadically, moving towards the dynamic game, and applying methods for computing effect size that use entire distributions rather than the mean and variance alone (which is what Cohen's *d* uses).

The canonical model developed here can be viewed as the first in a series of models of increasing complexity for understanding habitat selection (cf. Clark and Mangel (2000, Chapter 4)). Furthermore, first-person umwelt models move us towards answering the question of what it is like to be a non-human organism.

Methods

In the canonical problem for habitat selection, we envision a focal individual in a population of univoltine organisms in a seasonal environment. The annual cycle consists of a season in which individuals are born, gather resources for growth and future reproduction, and search for refuges, followed by a season in which the environment is harsh, and culminates with reproduction by individuals who survived the harsh environmental season. This description fits both deserts and temperate regions with appropriate interpretation of the seasons.

If the environment in the first season, when resources are gathered and refuges are sought, is sufficiently rich then we can assume that individuals accumulate all the resources needed to avoid starvation during the harsh environmental season and to reproduce at the end of that season (in the **Discussion** I discuss how to relax that assumption by including a state variable in the model). Searching for a refuge before the onset of the harsh environmental season thus becomes the task of individuals. The suitability of a particular refuge during the harsh environmental season is measured by quality *q* that determines the probability of surviving the harsh environmental season. Because this is a canonical problem, I do not give specific biological details about quality.

Search for an appropriate refuge commences at time $t = 1$ and must end before the onset of the harsh environmental season at $t = T$. At each discrete time, the focal individual encounters a potential refuge whose quality is drawn from a distribution (described below) and can either settle at the encountered habitat or continue searching.

Habitat selection is inherently a density dependent phenomenon (Northrup et al. (2022); McNamara and Leimar (2020)) because conspecifics are searching for habitats concomitantly with the focal individual. Thus the distribution of habitat quality changes from one time to the next. We finesse density dependence by specifying the time distribution of habitat quality (explained below).

While searching for suitable habitats, the focal individual experiences a constant probability of survival. Individuals who settle before *T* survive to reproduce depending upon quality of the refuge. Because of the assumption of a rich environment for resource gathering during the first season, at the end of the harsh environmental season all survivors are credited with the same level of reproduction (see **Discussion** for an alternative).

Mortality

We denote the probability of surviving a single interval of time by σ (if one prefers to think about the rate of mortality M, it can be determined from $\sigma = e^{-M}$, where the units of M are 1/time). When survival is independent across time intervals the probability of surviving to time t is σ^{t-1}. When $\sigma = 0.975$, as in the upper panel of Figure 2, survival to the time horizon $T = 45$ is just about 30%.

Survival during the harsh environmental season depending upon habitat quality

Survival is a key determinant of fitness and is often identified with fitness (e.g. Siepielski et al., 2009, 2017; Stroud et al., 2023); we follow that tradition for the canonical problem. We model the survival over the harsh environmental season of an individual settling in a habitat with quality q, $\mathcal{S}(q)$, as

$$\mathcal{S}(q) = \frac{e^{(q-q_{50})/\sigma_q}}{1+e^{(q-q_{50})/\sigma_q}} \quad (1)$$

The two parameters in Equation 1 characterize the quality giving 50% survival (q_{50}) and how sharply survival rises from small (close to 0) to large values (close to 1) as q increases (σ_q). For computations, I set $q_{50} = 0.75$ and $\sigma_q = 0.05$ (middle panel of Figure 2).

Distribution of habitat quality over time

We assume that at $t = 1$ the distribution of habitat quality follows a normal distribution with mean μ_{h} and standard deviation σ_{h}. For computations, I used $\mu_{\mathrm{h}} = 0.525$ and $\sigma_{\mathrm{h}} =$

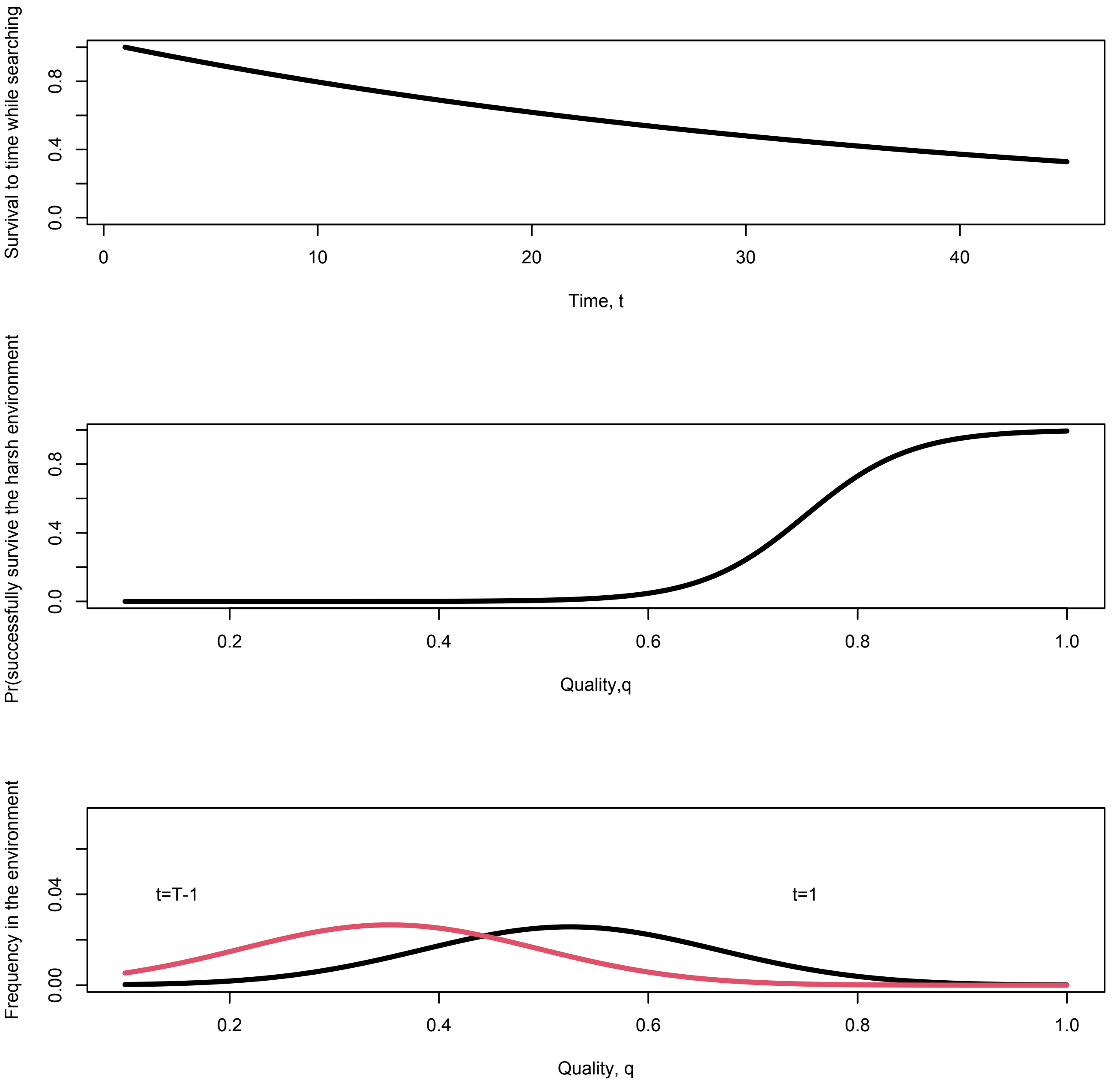

Figure 2. We characterize the environment by survival to time t of the focal organism when $\sigma = 0.975$ (upper panel), the probability of surviving the harsh environmental season as a function of quality of the settled refuge habitat, from Equation 1 with $q_{50} = 0.75$ and $\sigma_q = 0.05$ (middle panel), and the distribution of habitat quality at $t = 1$ (the beginning of the habitat selection process, black line) and $T - 1$ (red line) the time at which individuals have to settle to have any chance of surviving the harsh environmental season (lower panel). An individual will not survive the harsh environmental season unless it has settled in a refuge before T. These are sufficient for a third-person fitness optimization model using Stochastic Dynamic Programming.

0.2, and discretized habitat quality into 100 values between 0.1 and 1.0. If q_i and q_j denote any of these values, the initial probability of finding quality q_i in the environment is

$$f_0\left(q_i\right) = \frac{e^{-\frac{(q_i-\mu_h)^2}{2\sigma_h^2}}}{\sum_{j=1}^{100} e^{-\frac{(q_j-\mu_h)^2}{2\sigma_h^2}}} \quad (2)$$

In this equation, the denominator is a normalization condition; 100 discrete habitat qualities is sufficient to make the visual presentation look continuous. Lack spatial structure in the environment is implicit in Equation 2.

Habitat selection is inherently density dependent because when another individual settles into a habitat that habitat is no longer available to the focal individual. Treating this completely requires a dynamic game [McNamara and Leimar (2020); **Discussion**]. To focus on the comparison between first- and third-person models, we assume that higher quality habitats disappear faster than lower quality habitats. In particular if $f(q_i, t)$ denotes the fraction of habitats with quality q_i at the start of time t, we assume that

$$f\left(q_i,t\right)=\frac{f_0\left(q_i\right)e^{-\delta q_i t}}{\sum_{j=1}^{100} f_0\left(q_j\right)e^{-\delta q_j t}} \quad (3)$$

where $\delta > 0$ characterizes the rate at which habitats disappear due to other individuals selecting them. Because δq_i increases as q_i increases, higher quality habitats disappear at a rate faster than lower quality ones. For computations, I used $\delta = 0.2$. Equation 3 keeps the Gaussian shape for the distribution of quality across habitats but shifts it to the left as time increases (lower panel of Figure 2).

The third-person fitness optimization model

Once the environment is specified, the third-person fitness optimization model implemented by Stochastic Dynamic Programming (SDP) follows directly. We let $F(t)$ denote the maximum expected survival from time t to the end of the harsh environmental season, given that an individual is alive and not settled at time t, where "expected" is taken over the stochastic processes of encountering habitats of different quality and surviving both mortality while searching and the harsh environmental season. Since T corresponds to the onset of the harsh environmental season and there is no chance of surviving from that time onward if the individual has not settled, $F(T) = 0$.

For times $t < T$, when an individual encounters a habitat of quality q, it can either settle in that habitat, thus surviving the harsh environmental season with probability $\mathcal{S}(q)$ or continue searching in the next time $t + 1$ given that it survives the current time t, which occurs with probability σ. When the focal individual continues to search and survives, its maximum expected survival to the end of the harsh environmental season given that it has not settled at the start of the next time is $F(t + 1)$. This verbal description translates to the following dynamical equation

$$F(t) = \textstyle\sum_q f(q, t) max[\mathcal{S}(q), \sigma F(t + 1)] \quad (4)$$

The terms on the right side of Equation 4 are respectively the probability of encountering a habitat with quality q in search during time t, the probability of surviving to the end of the harsh environmental season given the individual settles, and the product of surviving from time t to time $t + 1$ and the maximum expected survival from time $t + 1$ to the end of the harsh environmental season. If $\mathcal{S}(q) \geq \sigma F(t + 1)$, we predict that the individual will settle (in the case of a tie, there is no reason for the individual to subject itself to the additional risk of mortality), otherwise we predict that it continues to search.

Since $F(T) = 0$, at time $t = T - 1$ the individual is predicted to settle into any habitat that it encounters. For previous times, there will be a threshold quality $q^*(t)$ with the property that the individual settles if the encountered quality q is at least the threshold and continues searching otherwise.

I show the boundary for acceptance of a habitat in time/quality plane in the upper panel of Figure 3. The boundary curve is a rule guiding the behavior of the organism and shows a slow broadening of the range of acceptable qualities until close to the time horizon. As T is approached, a wider range of habitat quality becomes acceptable, until at $T - 1$ we predict the individual will settle in any habitat. The shape of the boundary conforms with intuition: early in the search for refuges we anticipate that individuals will be choosier than when very little time remains. The precise shape of the boundary curve will, in general, depend upon the parameters in Equation 4. These are σ, characterizing survival during search, q_{50} and σ_q, characterizing survival during the harsh environmental season, and μ_h, σ_h, and δ, characterizing the distribution of habitat quality in the environment. If survival during search was lower, we expect individuals to be less choosy and that the relatively flat part of the boundary curve would be lower, but it is much harder to intuit how the boundary curve varies with the other parameters. Such a full sensitivity analysis is beyond the scope of this paper because of our objective is to compare first-person and third-person models. For an example of such sensitivity analysis in third-person models of parasitoid oviposition behavior see Chapter 4 in Clark and Mangel (2000).

In nature, we cannot observe the threshold boundary. Rather we observe the behaviors of individuals following the rule shown in the upper panel of Figure 3. Monte Carlo simulation forward in time (Mangel and Clark, 1988; Clark and Mangel, 2000) allows us to simulate data similar to that which could be collected by empirical observation.

In brief, the forward Monte Carlo simulation proceeds as follows. We simulate a large number N of individuals and track

- Whether individual n is alive or not at time t;
- whether the individual has settled or not at time t;
- the time of death if it is not alive, and
- the time of settlement (if it has settled).

When the time horizon is reached, each individual who has settled has probability of surviving the harsh environmental season determined by Equation 1, replacing q by q_n, which is the quality of the habitat into which individual n settled. The lower panels of Figure 3 show histograms of the time of settlement (for those individuals who survived until settlement) and the time of death (for those individuals who died before settlement) from an initial population of 1000 simulated individuals. The mean times of settlement and death are 9.6 and 11.1 respectively for the run of the simulation shown. It will be seen that these distributions generated by the stochastic processes characterizing survival are key to assessing convergence of the first- and third-person models.

The first-person umwelt model

Budaev et al. (2019) and Giske et al. (2013, 2014) give introductions (less and more technical respectively) to first-person umwelt modeling in behavioral and evolutionary ecology. Since these methods are not as well known as those used for third-person fitness optimization models, I develop the first-person umwelt model in more detail.

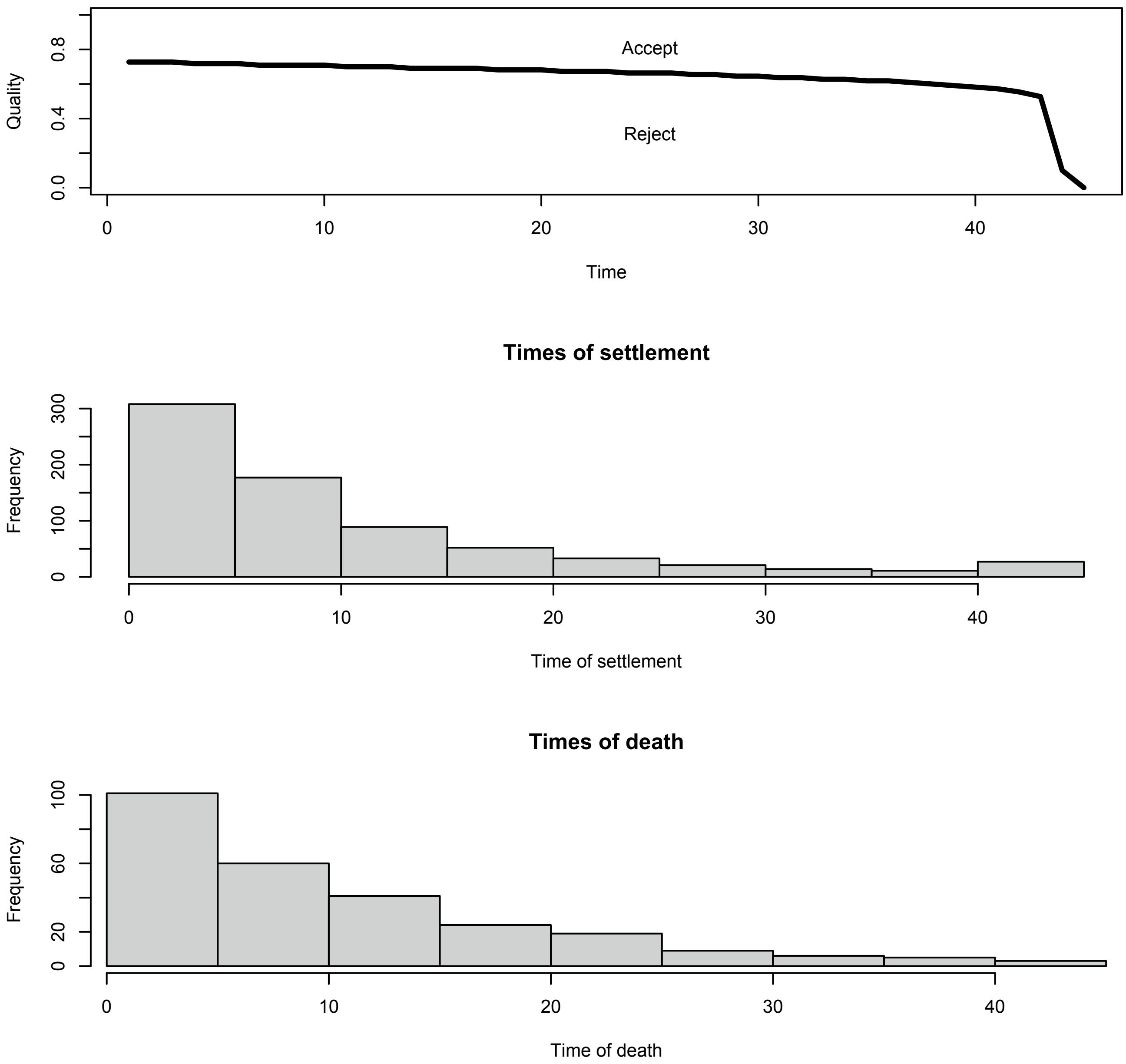

Figure 3. Upper panel: The SDP equation, Equation 4, generates a boundary in the time/quality plane that separates habitat qualities and times for which the individual is predicted to accept the encountered habitat from those in which it is predicted to continue searching. Middle and lower panels: Time of settlement (middle) and the time of death (lower) from an initial population of 1000 simulated individuals.

In the first-person umwelt model (Figure 4) an individual receives sensory signals from the environment (upper right of the figure) and its evolved neuronal networks (upper left of the figure) and assesses the sensory inputs (middle of the figure) to determine behavior (bottom of the figure). The behavior may influence the environment, and thus change future environmental signals. The response functions involve different physiological systems according to the organism and situation and are assumed to have an underlying genetic structure that responds to natural selection. When behavior affects survival and reproductive success, it can influence the genes and neurons determining the sensory response functions. For the canonical model, we do not model the neuronal networks explicitly (see Giske et al. (2014) and references there-in for details) but focus on the genetic architecture shaping the response functions and the evolution of the architecture.

For the canonical problem, we consider sensory responses to quality and time, and how to combine them to determine whether an individual continues searching or settles if it encounters a habitat of quality q at time t. The genetic architecture underlying a given behavior could be represented single genes, gene complexes, or a mixture of single genes and gene complexes (Gardiner et al., 1998) that evolve in response to environmental selection pressures. In our previous work [Giske et al. (2013, 2014), particularly the supplementary material, and Eliassen et al. (2016), particularly pg. 94ff] multiple genes evolve via sophisticated genetic algorithms. When many genes evolve in the genetic algorithm, the genotypic values are approximately continuous. Thus, for the canonical problem our starting assumption is that the genotypic architecture has continuous quantitative traits, so we characterize

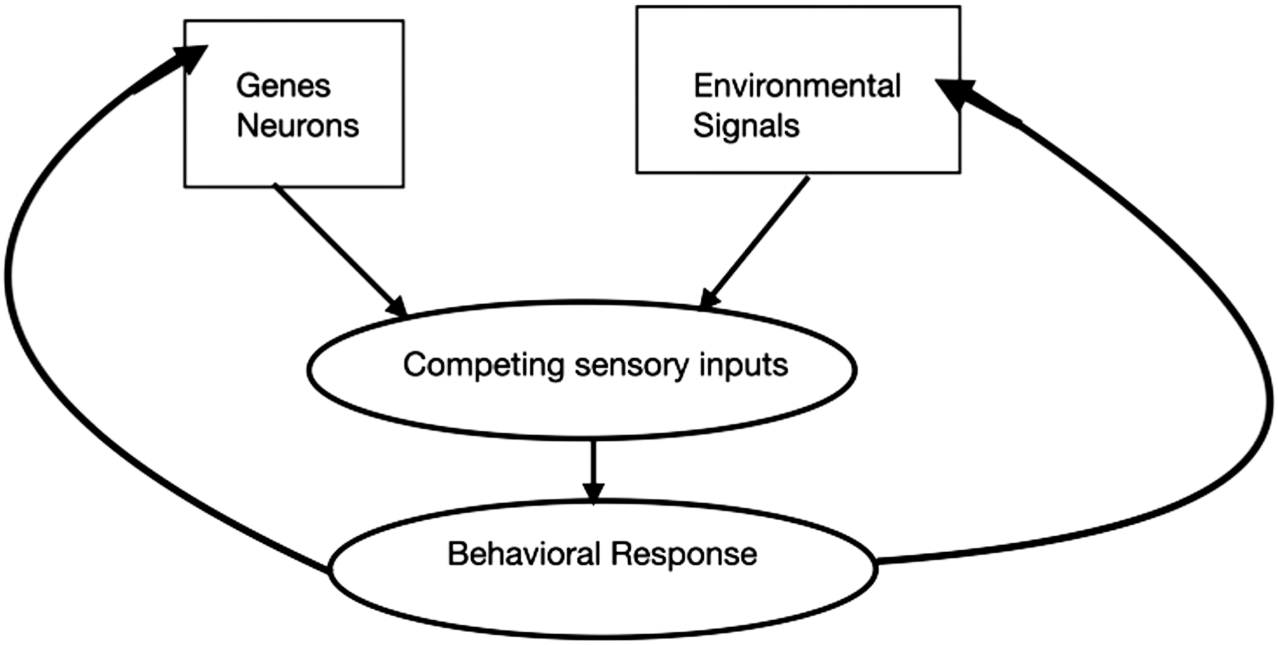

Figure 4. The basic structure of the first-person umwelt model. An individual receives sensory signals from the environment (upper right) and its own evolved neuronal networks (upper left) allowing assessment of competing sensory inputs (middle) from which a behavioral response (bottom) emerges. The behavioral response may influence the environment, and thus change future environmental signals. When the behavioral response affects survival and reproductive success, natural selection may change the genes determining the sensory responses.

the genotypes of offspring as the midpoint of the parental values, modified by random factors.

Sigmoidal response functions that range from 0 (no response) to 1 (response of maximum strength) are commonly used in neural network models (e.g. Marreiros et al. (2008); Rasamoelina et al. (2020); Sharma et al. (2020)). We also employed sigmoids in previous work on first-person modeling (Giske et al. (2013, 2014)) and I use them here.

Response functions for quality and time, and the propensity to settle

We let $R_q(q)$ denote the response to a habitat of quality q and assume that the response increases as q does. In particular, we assume that the response is determined by two components of the focal individual's genotype, denoted by x_q and y_q:

$$R_q(q) = \frac{q^{x_q}}{q^{x_q} + y_q^{x_q}} \quad (5)$$

Henceforth I will refer to x_q and y_q (and the analogous variables for time) as the X-gene and Y-gene for quality (in analogy, for time). For computations, I let the gene values range between 1.0 and 5.0. In previous work [Giske et al. (2013, 2014) or Budaev et al. (2018)], we used a complex genetic algorithm to determine the genes in the response functions. Assuming that the genotypes can be treated as quantitative traits simplifies the models of their evolution.

There are other ways to model sigmoidal functions, for example by replacing the power functions by exponentials, but the form shown in Equation 5 is long-tested and effective (Marreiros et al. (2008); Giske et al. (2013, 2014); Rasamoelina et al. (2020); Sharma et al. (2020)).

Inspection of Equation 5 shows that y_q is the value of quality q at which the response function is $R_q(q) = 0.5$. In the upper panel of Figure 5, I show the response for three values of x_q when y_q is fixed. In the lower panel, I show a heat map of the response in the quality/x_q plane, again with y_q fixed. The upper panel shows how the sigmoidal nature of the response depends upon the X-gene for quality and the lower panel gives a broad view of how the value of the X-gene and quality interact in a nonlinear way to shape the strength of the response.

We let $R_t(t)$ denote the response to time, measured by the organism's internal clock. I do not model the clock itself, but such genes have existed for a very long time (Seth, 2021). We assume a stronger response when considerable time remains, so that in analogy to Equation 5

$$R_t(t) = \frac{(T-t)^{x_t}}{y_t^{x_t} + (T-t)^{x_t}} \quad (6)$$

In this equation y_t is the value of time remaining time, $T - t$, that gives a 50% response. In Figure 6, I show the response to time for three values of x_t when y_t is fixed (upper panel) and a heat map in the time/x_t plane of the response function.

The Global Organismic State and probability of settling

An individual searching for habitat has an environmental and genetic state represented as a vector (t, q, x_q, y_q, x_t, y_t) and asks the question "Given the environmental and genetic state vector, should I settle or keep searching?" The

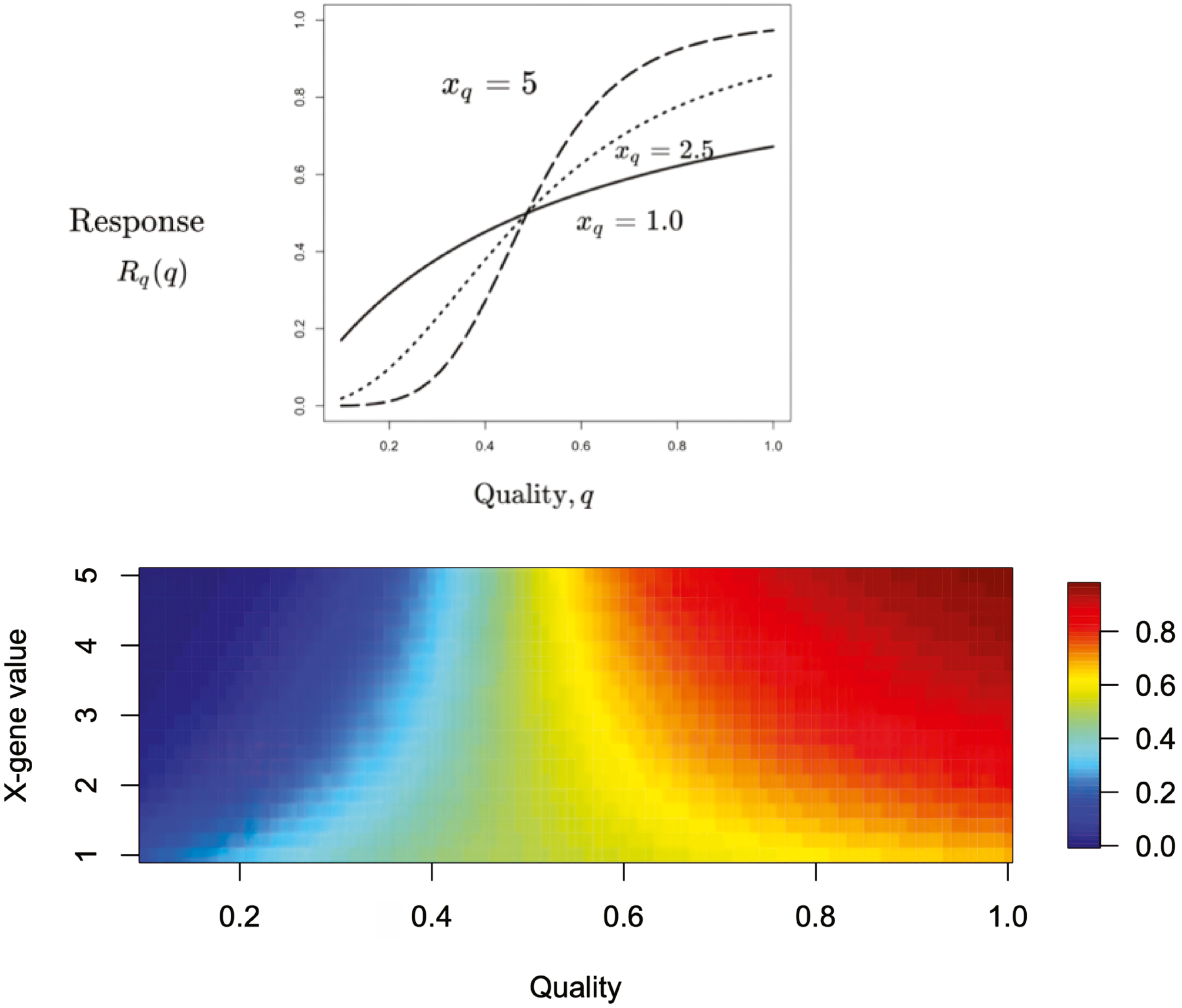

Figure 5. Upper panel: The response function $R_q(q)$ for three values of the X-gene x_q when the Y gene $y_q = 0.485$. Lower panel: A heat map of the response $R_q(q)$ in the quality/x_q plane, again with $y_q = 0.485$.

lower panels of Figures 5 and 6 suggest qualitative predictions. That is, imagine that $(t, q, x_q, y_q, x_t, y_t)$ puts the individual on the left side of both figures. Since the response to quality is low and the response to time is high we predict that the individual will keep searching. Similarly, if the $(t, q, x_q, y_q, x_t, y_t)$ puts the individual on the far right corner of both figures, the response to quality is high and the response to time is low and we predict the individual will accept the encountered habitat. But what would happen if the individual encountered a lower quality habitat, say around $q \approx 0.4$ when $t \approx 40$? Then it is not so clear what we would predict. Similarly, if time were between 20 and 30 and quality between 0.8 and 0.9, we need something more than eye-balling the figures to predict behavior.

To go beyond eye-balling figures to predict behavior, we need to represent the overall state of the organism in response to the signals. This is called the Global Organismic State [GOS; Budaev et al. (2019); Giske et al. (2025) and references there-in]. We capture the GOS by the difference in the response functions $R_q(q|x_q, y_q)-R_t(t|x_t, y_t)$, where the vertical lines remind us that the responses are conditioned on the genes. In the canonical model the GOS is the propensity to settle. For simplicity, I write $R_q(q)$ and $R_t(t)$ with the genes understood.

We use another sigmoidal function to convert the propensity to settle to a probability $p_{settle}(R_q(q), R_t(t))$ of settling in a habitat of quality q at time t given the responses $R_q(q)$ and $R_t(t)$. We assume that a strong response to quality increases the likelihood of settling and a strong response to time increases the likelihood of continuing to search so that the probability of settling is

$$p_{settle}(R_q(q), R_t(t)) = \frac{e^{[R_q(q)-R_t(t)]/\sigma_{settle}}}{1+e^{[R_q(q)-R_t(t)]/\sigma_{settle}}} \quad (7)$$

where σ_{settle} is another genetic parameter capturing the dispersion of the sigmoid. When σ_{settle} is much greater than $R_q(q) - R_t(t)$, the probability of settling is roughly 1/2 regardless of the value of the propensity to settle; when it is much less than the absolute value of $R_q(q) - R_t(t)$ the probability of settling will be close to zero or close to 1, rising sharply as the propensity traverses from negative to positive values.

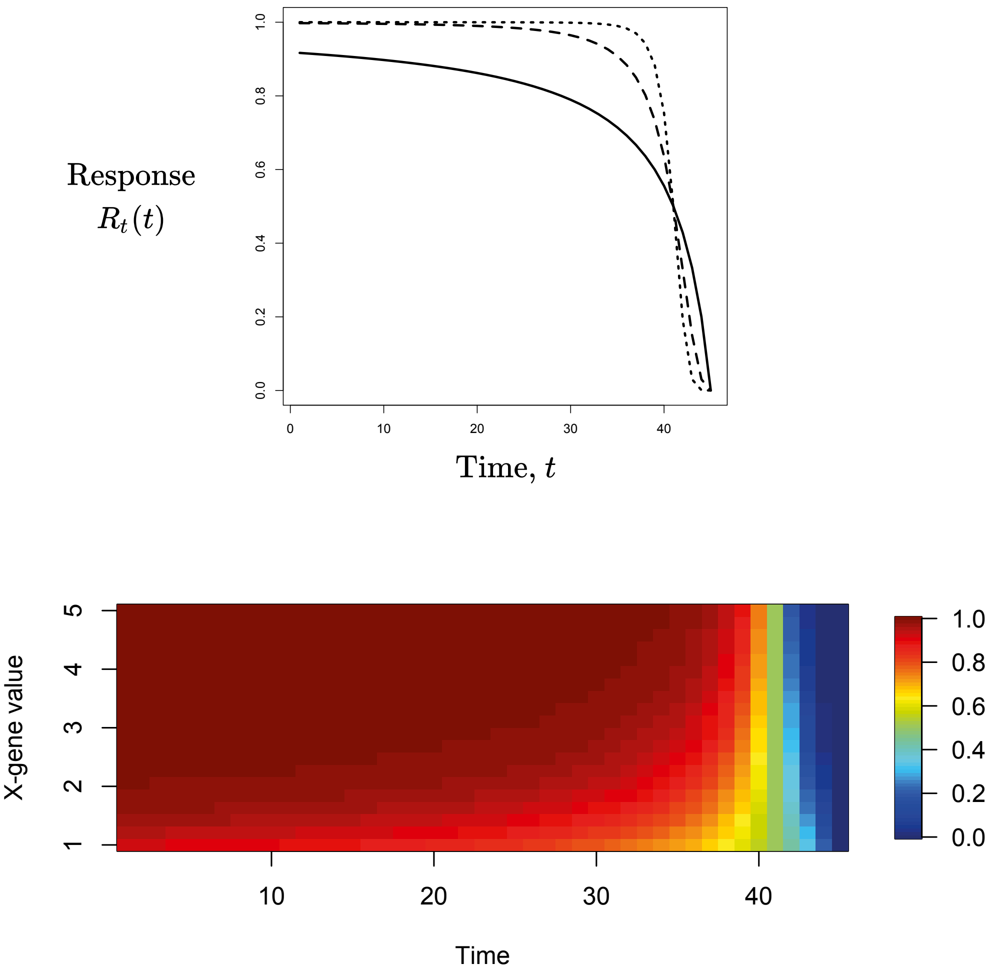

Figure 6. The analog of Figure 5 for the time genes. Upper panel: Three examples of $R_t(t)$ when $y_t = 4$, for $x_t = 1$, 2.5, and 5 (solid, long-dashed, and short-dashed lines respectively). Lower panel: A heat map of the response $R_t(t)$ in the time/x_t plane, again with $y_t = 4$.

The individual is now characterized by the five genes x_q, y_q, x_t, y_t and σ_{settle}. In order to keep comparisons between the first- and third-person models as simple as possible, I assume that y_q, y_t and σ_{settle} are rapidly fixed (the Y-genes at the values used above $y_q = 0.485$, $y_t = 4$, and $\sigma_{settle} = 0.1$). Doing so allows us to focus on the two X-genes, which is a complicated enough.

In Figure 7, I show heat maps in the time/quality plane of the probability of settling for eight randomly chosen combinations of the two X-genes. There are broad swaths in the time/quality plane where individuals will almost surely continue to search (the dark blue regions), and other areas (the upper right corners that are red) where individuals will almost surely settle. But the particular way these regions are joined varies according to the genes that an individual carries, and this will lead to variation in the acceptance of sites with moderate quality over time (the sky-blue bands).

It is straightforward to adapt the forward Monte Carlo simulation from the third-person fitness optimization model to the first-person umwelt model. The difference is that in the third-person model only a single population is simulated but in the first-person model we simulate across generations that are linked by dynamics of the genes. Because of the assumption of a rich resource environment during the season while searching, all survivors have the same number of offspring. In each generation, the forward simulation thus produces histograms analogous to those in the middle and lower panel of Figure 3. However, because survival over the harsh environmental season is determined by the genes of the parents, the genetic structure of the population will change from one generation to the next.

Evolution of the genes in the response function

The boundary curve produced by third-person fitness optimization model is the end point of evolution by natural selection. Indeed, one could imagine that the upper panel of Figure 3 is the result of the evolutionary competition between a large number of boundary curves, leading to one that provides the maximum survival of individuals carrying it, although doing this is not trivial in general (Gomulkiewicz and Beder, 1996; Beder and Gomuliewicz, 1998; Gomuliewicz et al., 2018). As a start, one could assume an asexual population, in which large number randomly chosen boundary curves are allowed to compete with each other across generations.

For the canonical problem, we model the evolution of the genes of the response functions in a sexual population as follows. Suppose that the number of individuals who

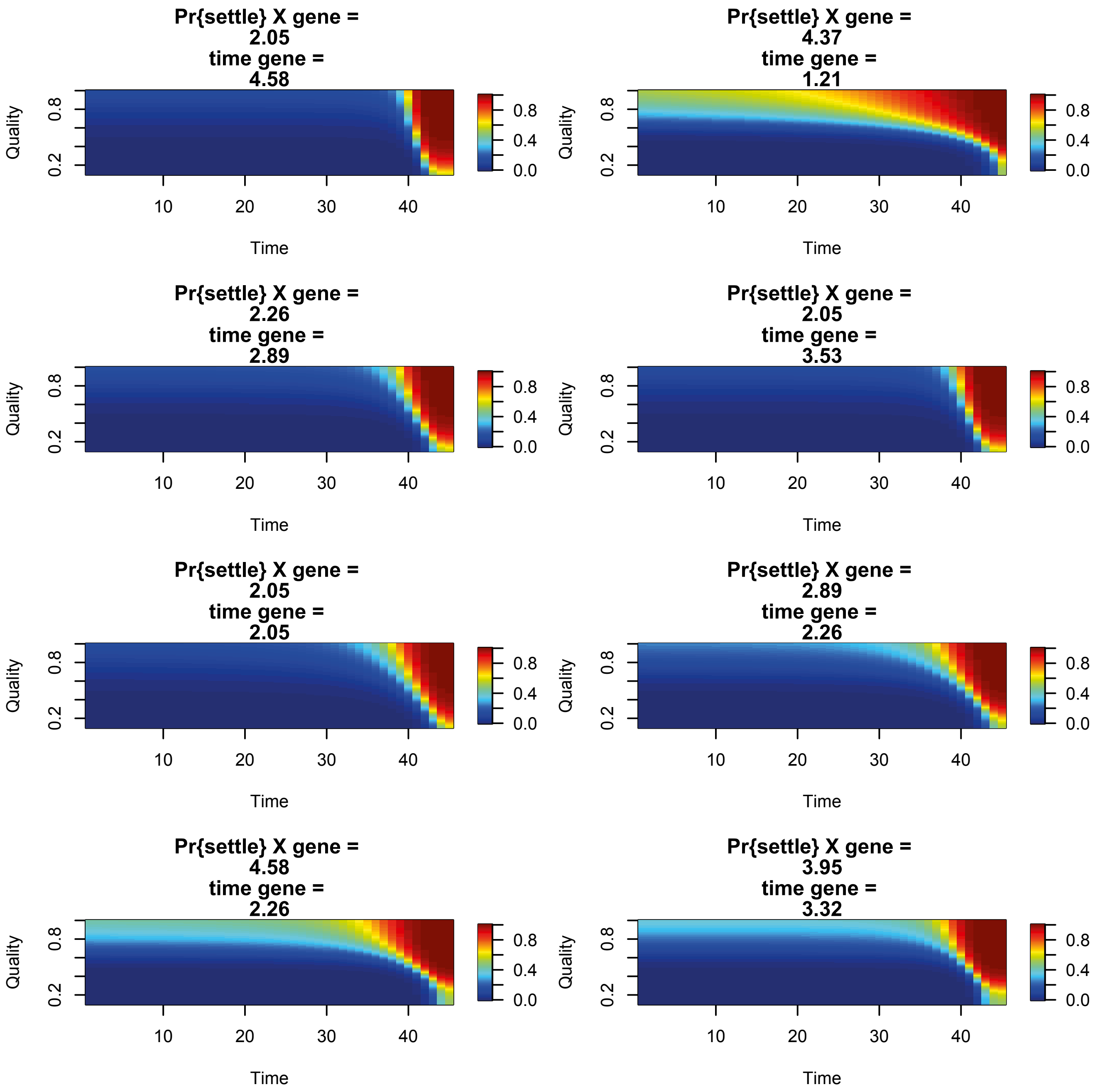

Figure 7. Heat maps in the time/quality plane of the probability of settling for eight randomly chosen combinations of the quality and time X-genes, with the Y- and σ- genes fixed.

survive the harsh environmental season is N_s. When individuals mate randomly, the number of breeding pairs N_p is the integer part of $N_s/2$. Now consider a generic pair of parents, whose quality and time genes are $(x_q(p_1), x_t(p_1))$ and $(x_q(p_2), x_t(p_2))$, where p_i denotes the i^{th} parent of the breeding pair. If $x_{q,off}$ and $x_{t,off}$ denote the quality and time genes of one of their offspring (all the other genes remain fixed across generations), we assume that

$$\begin{aligned} x_{q,off} &= \tfrac{1}{2}[x_q(p_1)+x_q(p_2)]+\sigma_{e,q}\mathcal{N}_{e,q}+\mu_{ga,q}(\mathcal{U}_q-0.5) \\ x_{t,off} &= \tfrac{1}{2}[x_t(p_1)+x_t(p_2)]+\sigma_{e,t}\mathcal{N}_{e,t}+\mu_{ga,t}(\mathcal{U}_t-0.5) \end{aligned} \tag{8}$$

In these equations, the left sides are the quality and time genes of the offspring and the terms on the right side are respectively the parental midpoint, a Gaussian modification of the parental midpoint where $\mathcal{N}_{e,q}$ and $\mathcal{N}_{e,t}$ denote normally distributed random variables with mean 0 and variance 1, $\sigma_{e,q}$ and $\sigma_{e,t}$ are mutational and environmental factors causing deviation from the parental midpoint; and $\mathcal{U}_{e,q}$ or $\mathcal{U}_{e,t}$ are uniformly distributed random variables on the interval [0,1] multiplied by an intensity factor $\mu_{e,q}$ or $\mu_{e,t}$ serving as a proxy for a full genetic algorithm. The first two terms on the right side are common; the third term allows for a higher probability of larger deviations from the parental midpoint and replaces a full genetic algorithm.

Assuming strong density dependence after reproduction but before the subsequent generation begins searching for refuges allows us to assume constant population size across generations. Since there are N_s survivors of the harsh environmental season and N_p breeding pairs, each breeding pair contributes at least the integer part of N/N_p to the next generation. There remain $N - N \cdot \mathrm{int}[N/N_p]$ places to fill in the next generation, and I allocate those sequentially across the offspring of the breeding pairs. For example, if 500 individuals are simulated per generation, when there are 288 survivors, and thus 144 breeding pairs, each breeding pair is assigned int[500/144]=3 offspring in the next generation. There remain 500-3·144=68 offspring to assign, so that in the next generation there are 4 offspring for the first 68 individuals and 3 offspring for the remaining 432 individuals.

Assessing the effect of evolution on survival and the convergence of the predictions of the first- and third-person models

For the first-person umwelt model alone, we can ask whether evolution of the genes in the response functions matters in the sense that survival in a subsequent evolved generation (we will use the 25th generation) is greater than survival in the initial generation in which the genotypes were randomly picked to initialize the simulation. Each run of the forward Monte Carlo simulation produces a single estimate of the fraction of individuals surviving, i.e. N_s/N.

Furthermore, each run of the forward Monte Carlo simulation of the first-person umwelt model generates frequency distributions of times of death and settlement in each generation, similar to those for the third-person fitness optimization model in the middle and lower panels of Figure 3. If the first-person umwelt model converges to the third-person fitness optimization model, we predict that the distributions of times of death or settlement in a subsequent evolved generation (also the 25th generation) will be closer in some sense to the distributions shown in Figure 3 than are the distributions of times of death and settlement in the initial generation when genotypes were randomly chosen.

We assess the effects of evolution of genes in the response functions and the convergence of the predictions of the first-person umwelt and third-person fitness optimization models using Cohen's *d* (Cohen (1988, 1994); Nakagaw and Cuthill (2007); White et al. (2013); Nakagawa et al. (2017); Methratta (2025)). The idea behind Cohen's *d* is extraordinarily simple, and the development in Cohen (1988, pg 19ff) is still one of the best. Imagine that we have two sets of data, denoted by Z_1 and Z_2, of lengths N_1 and N_2 respectively. When the samples, with means M_1 and M_2 and common variances V, are assumed to be independent, the two-sample t-test is a natural starting point for statistical tests of a difference between Z_1 and Z_2. Cohen (1988, pg 19) noted that in addition to assuming independence of the samples and equal (or nearly equal) variance, when using a t-test one assumes that the data are normally distributed. Cohen was working in behavioral sciences, in which the assumption of normality is far from assured and in which sample sizes may be wildly different, and was looking for an alternative to a statistical hypothesis test.

When the data come from an empirical source, whether observation or experiment, sample size will always be constrained. On the other hand, with a model sample sizes can be very large – indeed as large as one wants. This creates a difficulty with a t-test (or another other statistical hypothesis test) because we can always simulate a sufficiently large sample size to reject a null hypothesis of no difference. That is, because the power of a statistical test increases with sample size, any small difference eventually becomes statistically significant. Something other than standard statistical testing is needed for the comparison.

Cohen suggested that if we replace the assumed common variance by the pooled variance

$$V_{pool} = \frac{(N_1 - 1)V_1 + (N_2 - 1)V_2}{N_1 + N_2} \quad (9)$$

then the formula for the t-test is a measure of the difference in the means scaled by their pooled standard deviation. He called this the effect size and denoted it by *d*

$$d = \frac{M_1 - M_2}{\sqrt{V_{pool}}} \quad (10)$$

Cohen (1988) suggested that absolute values of *d* less than 0.2 are a small effect size, around 0.5 are a medium effect size, and greater than 0.8 are a large effect size; see Figure 2 in Methratta (2025) for illustration of these differences. Other authors suggest a finer division of the scale of effect sizes. For example, Sawilowsky (2009) proposed that effect sizes less than 0.01 are very small, around 0.2 are small, around 0.5 are medium, around 0.8 are large, around 1.2 are very large, and around 2.0 are huge. The crucial point is that Cohen's *d* standardizes the difference between the means by the pooled standard deviation and avoids formal hypothesis tests when they are not appropriate.

Since it requires all the replicates of the forward Monte Carlo simulation to generate single estimate of survival, we can compute only one value of Cohen's *d* to compare survival in the initial (random) and 25th (evolved) generations. However, since each replicate of the forward Monte Carlo simulation produces distributions of the times of death and survival, each replicate of the Monte Carlo simulation has its own value of Cohen's *d*.

Results

I first address the evolution of the genes in the first-person umwelt model, then whether survival increases due to the evolution of the genes, and finally, in what sense the predictions of the first-person umwelt model and third person fitness optimization models converge.

The genes evolve

In Figures 8 and 9, I show the distributions of the X-genes for quality and time in the first 12 generations when the additive genetic variances $\sigma_{e,q}$ and $\sigma_{e,t}$ are sufficiently high to maintain genetic diversity (Figure 8) or too small to maintain genetic diversity (Figure 9). In both cases, evolution from a uniform distribution of genes in the first

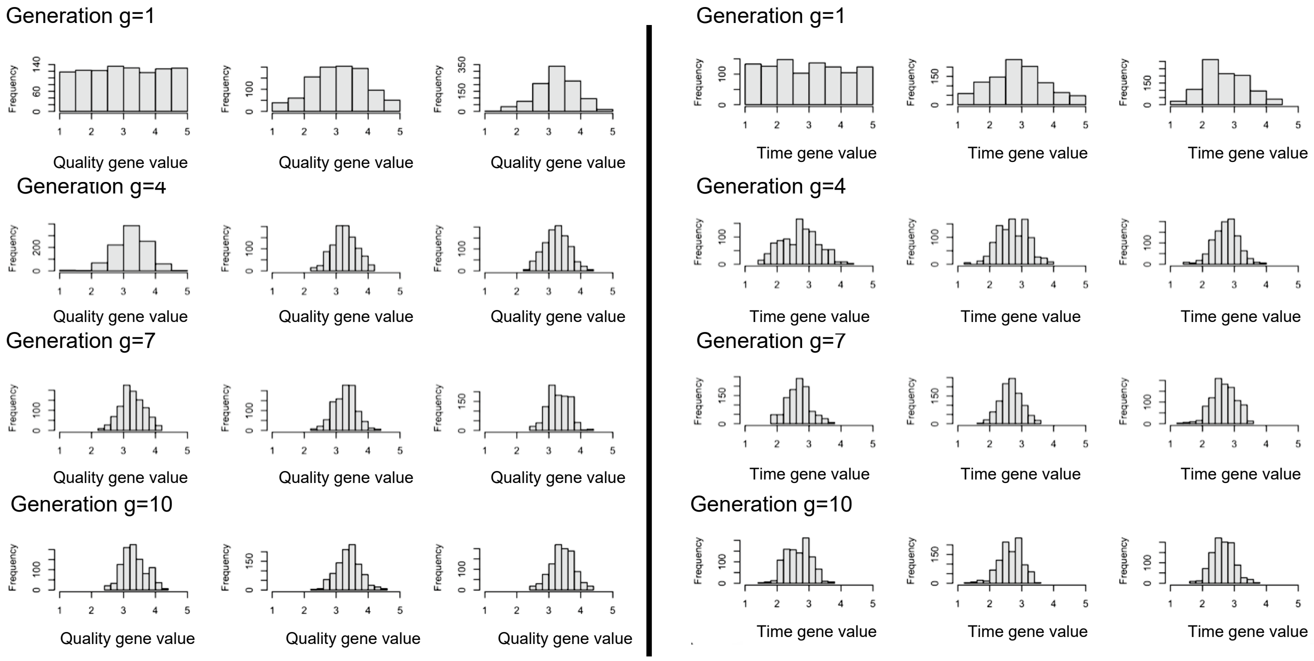

Figure 8. Example of the evolution of quality genes (left panels) and time genes (right panels) when $\sigma_{e,q}$ and $\sigma_{e,t}$ in Equation 8 are sufficiently high (both 0.25) to maintain genetic variation; $\mu_{ga} = 0.15$. Generation time runs across columns and then down rows in both plots. The initial distributions are realizations of uniform distributions.

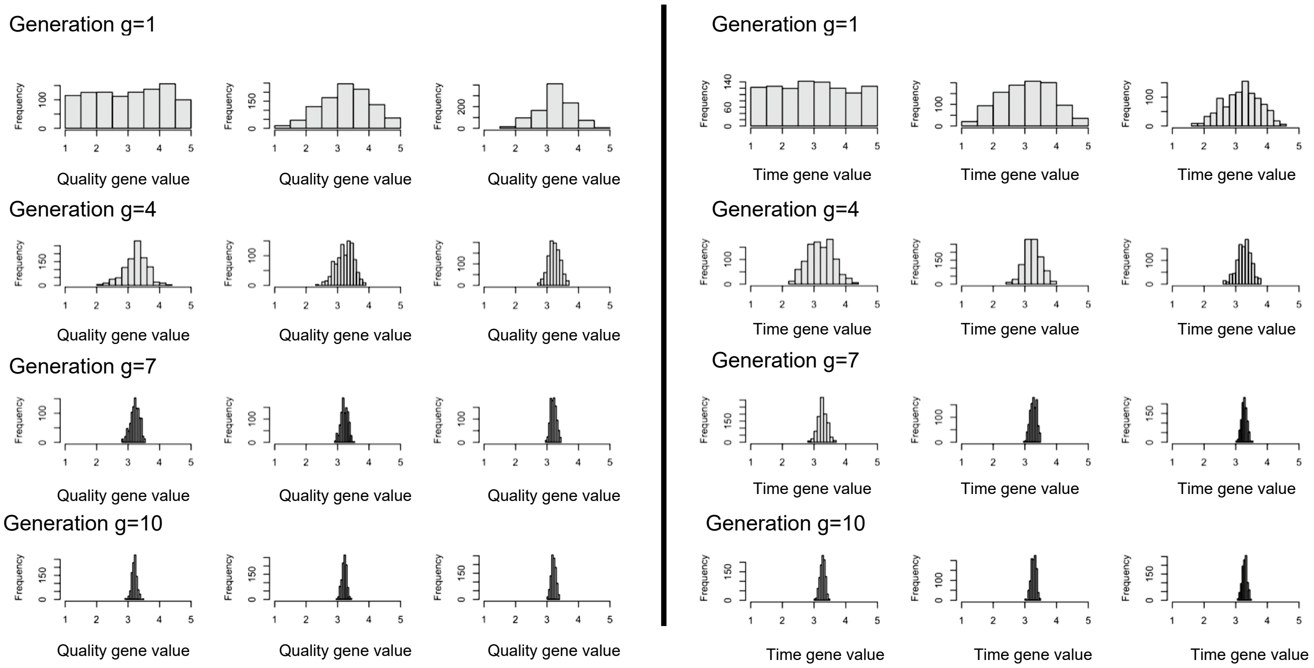

Figure 9. Example of the evolution of quality genes (left panels) and time genes (right panels) genes when $\sigma_{e,q}$ and $\sigma_{e,t}$ in Equation 8 are not high enough (both 0.025) to maintain genetic variation; $\mu_{ga} = 0.15$. Generation time runs across columns and then down rows in both plots. The initial distributions are realizations of uniform distributions.

generation is rapid towards a quasi-stable state; we return to why this occurs in the **Discussion**.

Strong selection removes extreme values of the genes, so that a peaked distribution that continues to fluctuate is quickly reached. I will refer to this as the quasi-steady state.

Evolution leads to increased survival

To assess whether evolution of the genes matters for fitness (survival) or not, we compare the fraction of individuals surviving in the first generation with the fraction of individuals surviving in the 25th generation. (Figure 10). In this figure, survival in the initial generation is clearly

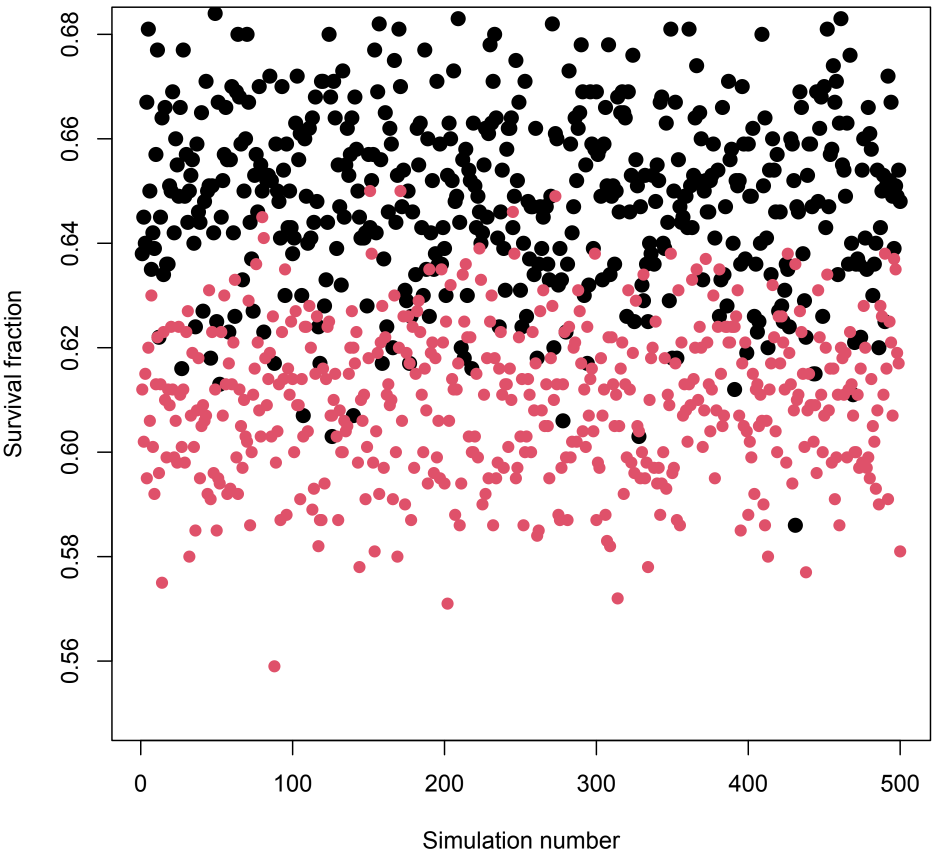

Figure 10. Each run of the full Monte Carlo simulation of the first-person umwelt model leads to a single value for the fraction of individuals surviving to reproduce. In this figure the fraction of survivors in the first generation is shown in red and the fraction of survivors after 25 generations is shown in black. In general, evolution of the genes determining the response functions leads to higher survival. The value of the effect size is $d = 2.3$, which is huge according to the classification of Sawilowsky (2009).

lower than in the evolved generation. The effect size $d = 2.3$ and "huge" according to the classification of Sawilowsky (2009).

Convergence of the first-person and third-person model predictions

From the initial to the 25th generation, Cohen's d for time of death declines by a factor of about 3 (Figure 11) and Cohen's d for the time of settlement declines by a factor of about 2 (Figure 12), with associated effect sizes that are small and medium respectively. Because of the rapid evolution to the quasi-steady state of the genes, we should not expect much additional improvement in Cohen's d if we waited longer in the evolutionary process.

Discussion

In the third-person fitness optimization model the probability of survival is specified (or in more complicated models, is given a distribution that is then updated over time) but in the first-person umwelt model, there is no assumption that the individuals know the probability of survival. The first-person umwelt model is thus very different than a Bayesian model of learning, in which individuals begin with an inherited probability distribution that is updated over time (Mangel, 1993). At the end of the evolutionary trajectory in the first-person umwelt model, the individuals in the current generation have no more knowledge about the distribution of the probability of survival (or the specific value) than their ancestors. It remains to be seen how the computational complexities of a Bayesian model of learning and the first-person umwelt model compare.

In changing environments, third-person fitness optimization models give the endpoints of evolution in response to the changed environment. Thus, we can predict how behavior and reproductive success ultimately respond to a change in environmental conditions if there is sufficient genetic variation but not whether the new evolutionary endpoint will be reached or how and when it will happen (Sattherthwaite et al. (2010)). On the other hand, the first-person umwelt model provides that information generation by generation, as the genes of the response functions evolve due to the changing environment.

Furthermore:

- The improvement in survival with the evolved genes suggests that we have a generally good model and the speed with which the quasi-steady state distribution of

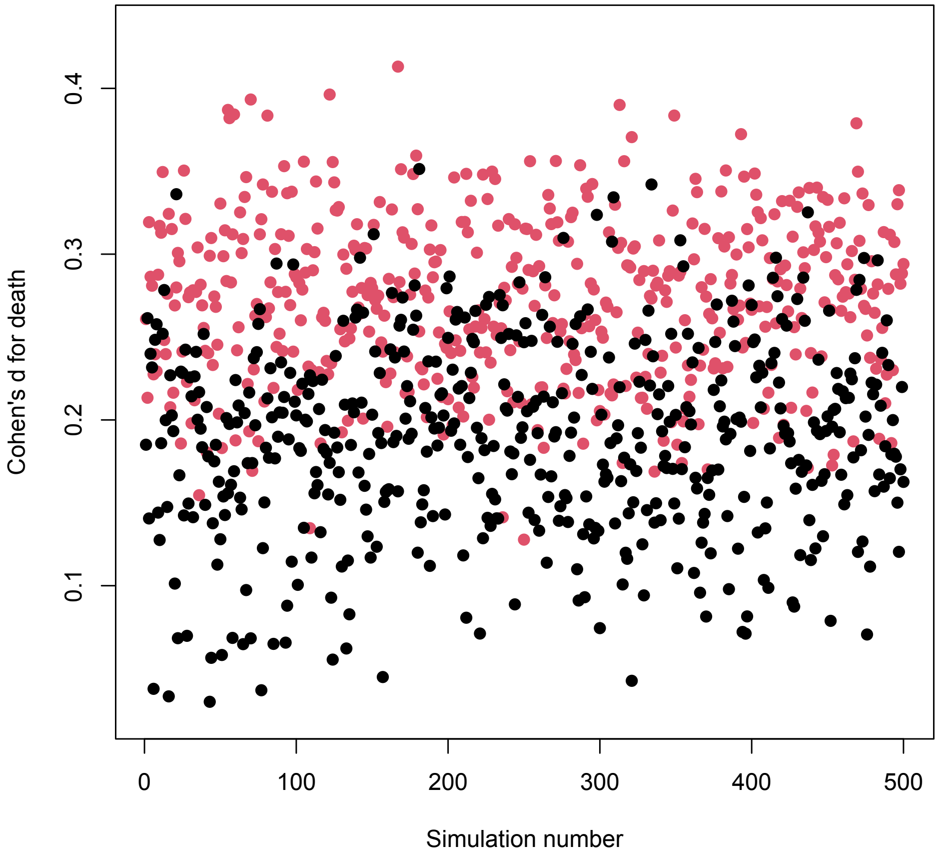

Figure 11. Convergence of the predictions of the first-person umwelt and third-person fitness optimization models by comparing distributions for the times of death for the simulation of the first-person umwelt model to those in Figure 3 for each iterate of the simulation. The red circles show the value of Cohen's *d* in the first generation and the black circles show the value of Cohen's *d* after 25 generations.

genes is reached is likely due to the (intentionally) low complexity of the canonical problem. If we allowed the Y-genes and σ_{settle} to evolve as well, it is likely that even smaller values of effect size could be obtained but also that the genetic landscapes become more complex and rugged.

- It is natural for quality to have multiple characteristics. For example, the quality of a burrow for a desert insect might depend upon depth (q_1), temperature (q_2), and humidity (q_3). This suggests replacing Equation 11 by a weighted sum of response functions

$$R_q(q_1,q_2,q_3) = \sum_{i=1}^{3} \frac{\omega_i q_i^{x_{qi}}}{q_i^{x_{qi}} + y_{q_i}^{x_{qi}}} \quad (11)$$

- where the ω_i sum to 1 and measure the importance of that aspect of quality to the overall response. Eliassen et al. (2016) explored a version of Equation 11 and found that for the ecological scenario they modeled – a small fish moving vertically in the water column in response to hunger and predators – the behaviors based on the simpler or more complicated response function were generally the same. It remains an interesting empirical question to ask how multiple factors that determine quality can be blended in the best way in the response function.
- A stronger response to quality indicates that the organism is more likely to settle in the current habitat. Giving a third-person perspective to this first-person response, we might say that the response tells us how the individual "feels" about the quality of the currently encountered habitat. A stronger response to time means that the individual is more likely to continue searching. From a third-person perspective, this response tells us how the individual "feels" about survival in the environment. We are thus modeling feelings or emotions and providing a canonical mechanism for how they are made (Feldman Barrett, 2017). Since habitat quality and probability of survival both influence settling behavior, it may be possible to gauge how survival is perceived by the individual through its behavioral response to habitat quality.

Some future directions

Extensions of the canonical model include:

Adding a state variable. In order to keep the models as simple as possible, I assumed that the state, e.g. weight of the focal individual denoted by $W(t)$ with specific value w, was constant. This was the main role of the rich environment during the season in which individuals search for a refuge. For higher fidelity to nature, one could assume

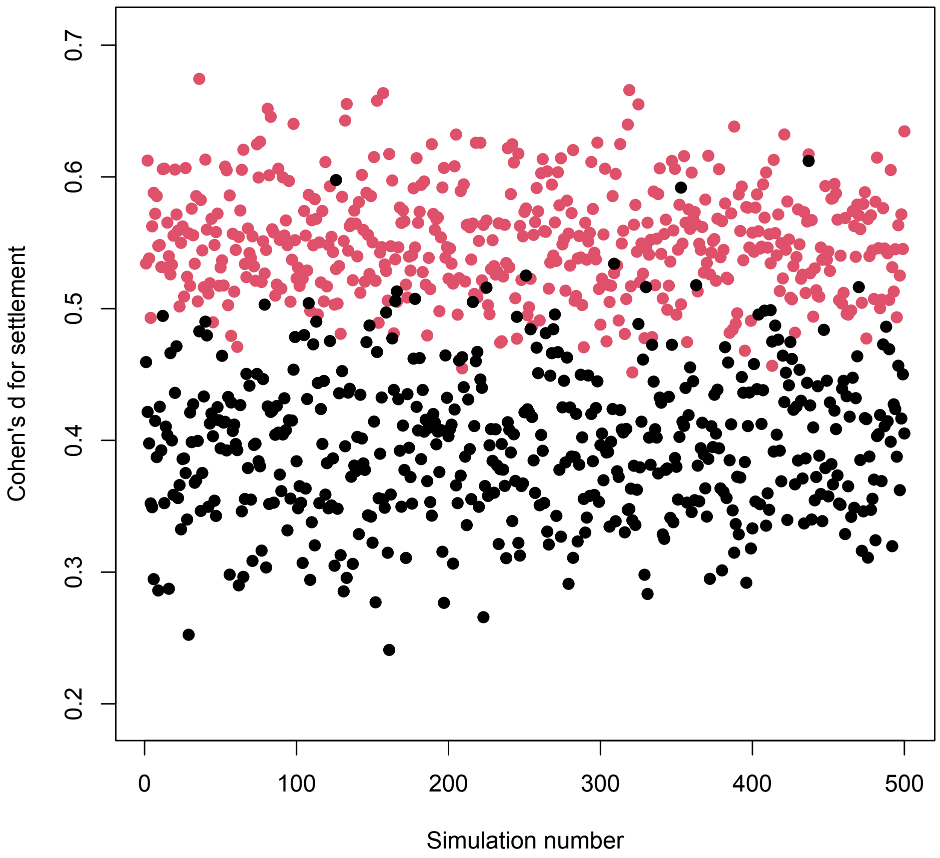

Figure 12. The analog of Figure 11 for the times of settlement.

that weight declines during search and time in the refuge. Even higher fidelity could assume stochastic increases in weight, as in the patch selection model of Mangel and Clark (1988). If the state dynamics were a decline by an amount c_1 during each time interval of search and by c_2 after settlement, before the individual settles the dynamics of the state are

$$W(t+1) = W(t) - c_1 \quad (12)$$

with $W(1) = w_0$ specified. After settlement, the dynamics are similar to those in Equation 12 with c_1 replaced by c_2.

If an individual settles at time t, its state at the end of the harsh environmental season will be $w_0 - (c_1t + c_2(T - t))$. Assuming that Survival is proportional to relative weight at the end of the harsh environmental season, the Survival $\phi(t, q)$ of an individual who settles into a habitat of quality q at time t is then

$$\phi(t,q)=\mathcal{S}(q)\left(1-\frac{c_1t+c_2(T-t)}{w_0}\right) \quad (13)$$

We then replace $\mathcal{S}(q)$ by $\phi(t, q)$ in both Equation 4 and the forward Monte Carlo simulation in the first-person umwelt model.

Reproductive success depending on quality of the habitat. Equation 13 accounts for survival depending upon state in a very simple manner and quality of the habitat into which the individual settles, but offspring production is still constant across survivors. When the number of offspring produced $\mathcal{O}(q)$ depends on quality q of the habitat, we need to separate males and females because males may simply have to survive the harsh environmental season to reproduce, whereas offspring production by females may depend on habitat quality differently than survival. In this case, in the third-person fitness optimization model we require potentially separate SDP equations for male and females, even if random mating occurs. The logic of the first-person umwelt model remains unchanged until reproduction, but there will be many other modeling choices that have to be made about the details of reproduction.

Additional sources of mortality. In addition to the background mortality some environments may include an occasional source of secondary mortality. In that case, σ in Equation 4 can be interpreted as the background mortality; we introduce the probability $p_s(t)$ that a secondary predator is present at time t and the probability σ_s of surviving the secondary predator. The straightforward extension of Equation 4 is

$$F(t) = \textstyle\sum_q f(q, t)[(1 - p_s(t))max(\mathcal{S}(q), \sigma F(t + 1)) \\ + p_s(t)max(\mathcal{S}(q), \sigma_s\sigma F(t + 1))] \quad (14)$$

Equation 14 generates two boundary curves in the time/quality plane, corresponding to whether the secondary predator is present or not.

Two responses to time will be required in the first-person umwelt model, with Equation 6 applying when there is no signal of a secondary predator. When a signal of the secondary predator is received, we add a modifier gene z_t to Equation 6

$$R_{t,s}(t) = \frac{z_t(T-t)^{x_t}}{y_t^{x_t}+(T-t)^{x_t}} \quad (15)$$

As long as z_t is less than 1 the response when a signal of the secondary predator is received will be weaker than in the absence of the signal, and thus the focal individual will be more likely to settle.

Moving towards the dynamic game. For the third-person fitness optimization model, a method for treating the dynamic game is well known but rarely trivial [McNamara and Houston (1999); Clark and Mangel (2000); Alonzo et al. (2003) for a particular application]: One iterates between the solution of the SDP equation and the forward Monte Carlo simulation. On the first iteration, we proceed exactly as above when solving the SDP equation. After the forward iteration, we replace the distributions of habitat quality in Equation 3 by those that emerged from the forward Monte Carlo simulation and then resolve the SDP equation and forward simulate behavior once more. This procedure is repeated until it stabilizes, in the sense that the best response to the distribution of habitat quality over time generates, to within reasonable errors, the distribution of habitat quality over time used in the SDP generating the boundary curve.

Refine comparisons using Hellinger distance. Since Cohen's *d* relies on means and variances only, it does not take full advantage of the distributions produced during the forward Monte Carlo simulations. An alternative is Hellinger's distance [Hellinger (1909); Cha (2007); Ditzler and Polikar (2011); Warren et al. (2008)], which compares properties of full distributions. For a canonical problem Cohen's *d* is a good choice, but Hellinger's distance will likely be a better tool for comparisons when first-person umwelt and third-person fitness optimization models are developed for particular species in particular situations.

Conclusions

The canonical model for habitat selection developed as a third-person fitness optimization model continues a long tradition of successful third-person modeling in behavioral and evolutionary ecology. The first-person umwelt model has higher fidelity to the means by which behavior is determined and complements the third-person perspective. Neither is intended to model a particular organism in a particular situation. Rather, both are intended to capture the essential idea of habitat selection and by further development be applied more specifically. In this regard, they can be viewed as the first of a series of models of increasing complexity that allow us to focus on questions of increasing complexity [see Clark and Mangel (2000, Chapter 4) for the development of such a series of models for parasitoid oviposition behavior]. Both first-person umwelt and third-person fitness optimization models will contribute to deeper understanding of the natural world. Indeed, a most exciting prospect is to envision empirical data concerning particular organisms in particular situations complemented by the development of both first-person umwelt and third-person fitness optimization models and the subsequent confrontation of models and data.

Neither Leon nor I knew of Nagel (1974) when we first worked together. However, I can easily imagine conversations in which Leon might have mused that "I want to know what it means to be a mosquito" or "I want to know what it means to be a *Salamandra* (fire salamander)". Models using the first-person umwelt perspective have great potential to answer these questions, and similar questions for organisms as diverse as desert isopods (Zaguri et al. (2018); Zaguri and Hawlena (2020)), octopuses (Hanlon and Messenger (1996/2003); Mather et al. (2010)), or salmon (Budaev et al. (2024); Giske et al. (2025a)).

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